OLENELLUS (TRILOBITA) FROM THE LOWER CAMBRIAN STRATA OF NORTH-WEST SCOTLAND

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ABSTRACT. New material of *Olenellus lapworthi*: Peach and Horne, 1892, *O. reticulatus* Peach, 1894, and *O. intermedius* Peach, 1894, enables redescription of these forms and illustration by photographs for the first time. *O. gigas* Peach, 1894 is suppressed and *O. hamoculus* sp. nov. is erected. Graphs are used to illustrate the relationships established. The fauna represents the younger part of the *Bonnia–Olenellus* Zone in the Pacific Province of the Olenellid Realm.

THE Cambro-Ordovician outcrop of north-west Scotland is about 200 kilometres long and varies in width between 2 and 20 kilometres stretching from Durness in the north to Skye. The Cambro-Ordovician beds were evidently laid down in a sea which gradually transgressed across older, Precambrian, strata, resting with angular unconformity on them. Total thicknesses are not well known, partly due to the nature of the outcrops and the involvement of the strata in a major thrust-zone. The olenellid-bearing formations are the 'Fucoid' Beds (12–27 m thick) and the overlying *Salterella* Grit (5–15 m thick).

The 'Fucoid' Beds are dolomitic siltstone or shale, arenaceous dolomites, arenaceous dolomitic mudstones, and grits with ripple-induced micro-cross-laminations; in places thin limestones and lenticular dolomitic sandstones occur; the weathering is characteristically brown to buff and ferruginous in colour. Swett (1969, p. 645) considered that the 'Fucoid' Beds were deposited in shallow to moderately deep water on an ever-broadening shelf at increasing distances from the detrital sources.

Thin series of beds of grey siltstone, arenaceous shale or shale, which weather rusty-brown, are the main source of olenellid trilobite remains which are generally disarticulated exuviae, though occasional articulated specimens have been found. The specimens are generally preserved as internal and external moulds. Due to the very thin nature of the exoskeleton there are no significant differences between internal and external moulds, apart from the presence of the ornament on the external mould, though in some instances it has been impressed through to the internal mould (Pl. 70, fig. 12). Fossiliferous horizons occur at several levels in the 'Fucoid' Beds (Brand 1965).

The *Salterella* Grit is a thin persistent grit formation predominantly made up of quartzite, orthoquartzitic sandstone containing minor detrital carbonate grains, arkosic grit, dolomitic sandstone and sandstone, but there are interleavings of shales near the base which give *Olenellus lapworthi*. The fossil collections are meagre compared with those from the 'Fucoid' Beds.

The first specimens of trilobites from Scotland assignable to *Olenellus* were collected in the late nineteenth century by M. Macconochie, a member of the Geological Survey team led by B. N. Peach and his colleagues. The trilobites came from Allt

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nan Righreon (Allt Righ Ian) in the Dundonnell Forest, Ross and Cromarty (Peach and Horne 1892, p. 228) (text-fig. 1). Around the turn of the century further discoveries of olenellid trilobites were made along the north-west Scotland outcrop strip of the Fucoid Beds and *Salterella* Grit (see text-fig. 1).

Localities mentioned in the text and shown on text-fig. 1 are An-t-Sron, Loch Eriboll (1), Skiag Bridge (2), Loch Awe quarry (3), Knockan Cliff (4), Allt nan Righreon and Loch an Nid (5), Meall a'Ghiubhais, Kinlochewe (6), and Ord, Skye (7).

In the 1960s and 1970s new collections of olenellid trilobites were made by the Institute of Geological Sciences (Bowie *et al.* 1966; Brand 1965) and by John Cowie, Kenneth McNamara, Susan Radford, and John Branegan from various localities including especially the recently excavated roadstone quarry at Loch Awe, south of Inchnadamph, Ross and Cromarty (see above and text-figs. 1–3). Descriptions and illustrations of some of the fossils dealt with in this paper were published by Peach and Horne (1892), Peach (1894), Peach *et al.* (1907), Walcott (1910), and Lake (1937) but in these earlier works only drawings were used without photographs.

The purpose of this paper is to redescribe the species in the light of the new discoveries at Loch Awe, and to describe a new species, *Olenellus hamoculus*. Specimens were qualitatively designated; significant variable features were then measured and plotted on graphs (text-figs. 2, 3) to illustrate the relationships established.

Descriptive terminology and techniques. Terms used in the systematic descriptions follow Harrington *et al.* (*in* Moore 1959) except that the terms 'extra-ocular area' and 'inter-ocular area' are used in place of 'gena' (Moore 1959, p. O120); 'intergenal spine' is preferred to 'metagenal spine'. One new term, 'epipalpebral furrow', is introduced to describe the longitudinal furrow in the eye lobe.

The parameters plotted in text-figs. 2 and 3 are associated with those morphologic features which are often described as being of specific significance among olenellids, e.g. relative length of eye lobe (text-fig. 2*a*, *b*), glabellar shape (text-fig. 3*a*), relative length of preglabellar field (text-fig. 3*b*).

Text-fig. 3*b* shows that the relative sagittal length of the cephalon and preglabellar field has little specific importance when differentiating between these three olenellids. Text-fig. 2*a* and *b* illustrate the importance of eye length, whilst text-fig. 3*a* shows how the glabella shape can vary interspecifically.

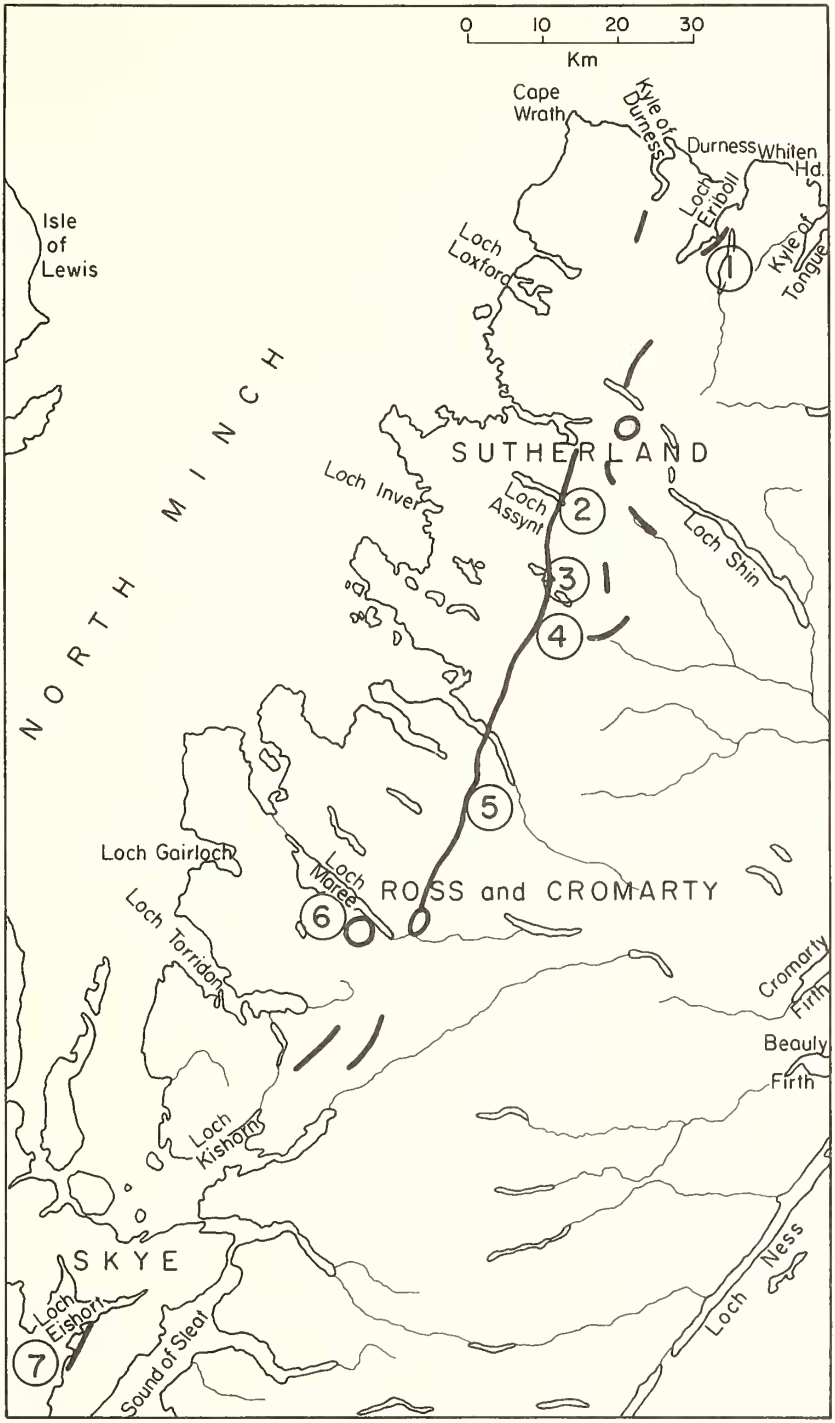
The number of specimens measured, *n*, varies due to some cephala being incomplete so that not all parameters were obtainable.

All measurements were made with eye lobes in a horizontal plane.

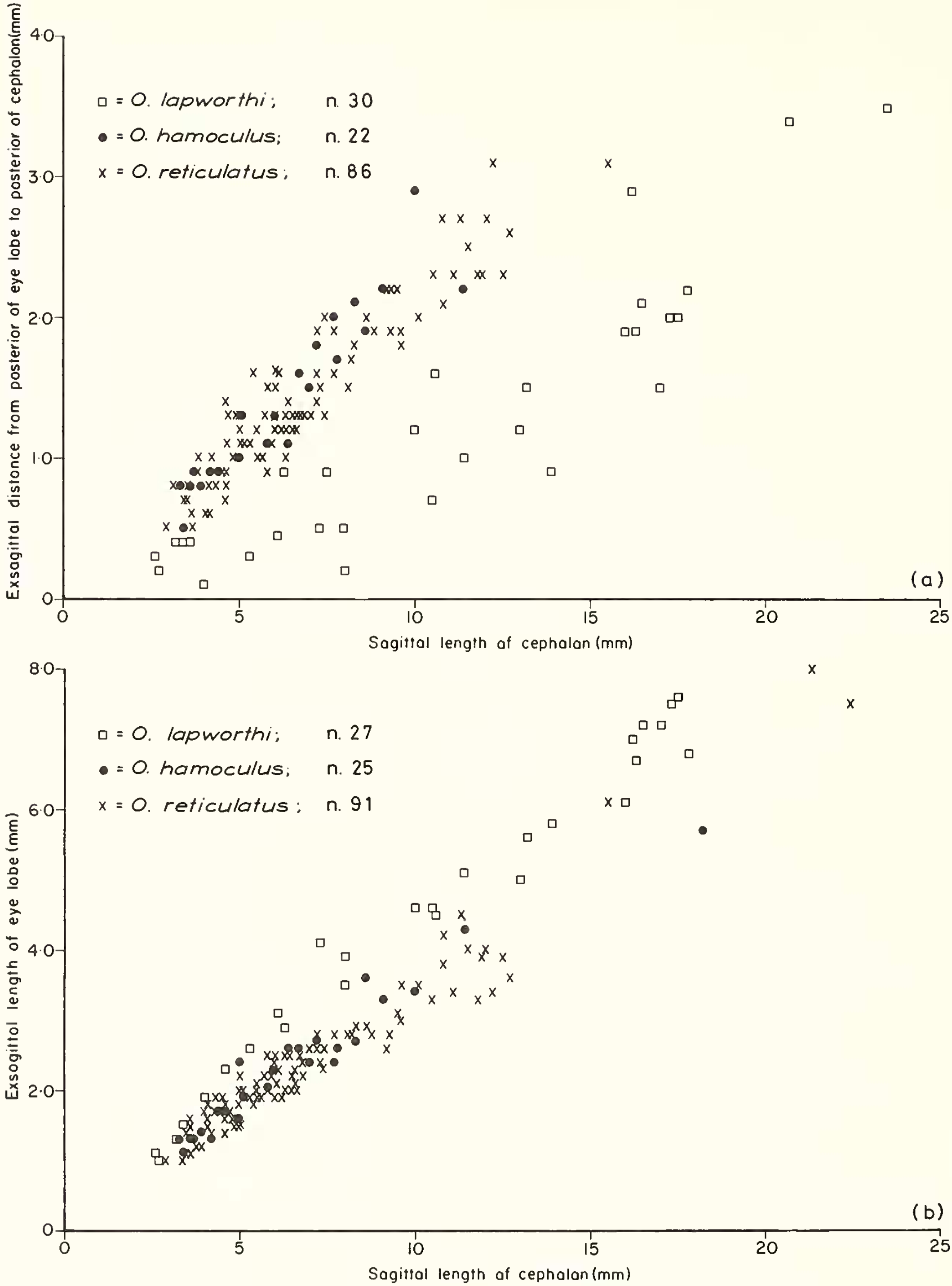
Associated faunas and the zone represented

In addition the fauna includes: the trilobite *Olenelloides armatus*, Peach; the brachiopods: *Micromitra* sp., *Lingulella zeus* Walcott, *Paterina* sp., *Kutorgina* sp., *Acrothele subsidua* White, the gastropod *Murchisonia*? sp.; miscellanea: *Hyolithes* sp., *Salterella* spp., *Coleoloides* sp., echinodermata ind., crustacea ind., and the worm trace fossil *Planolites* sp.

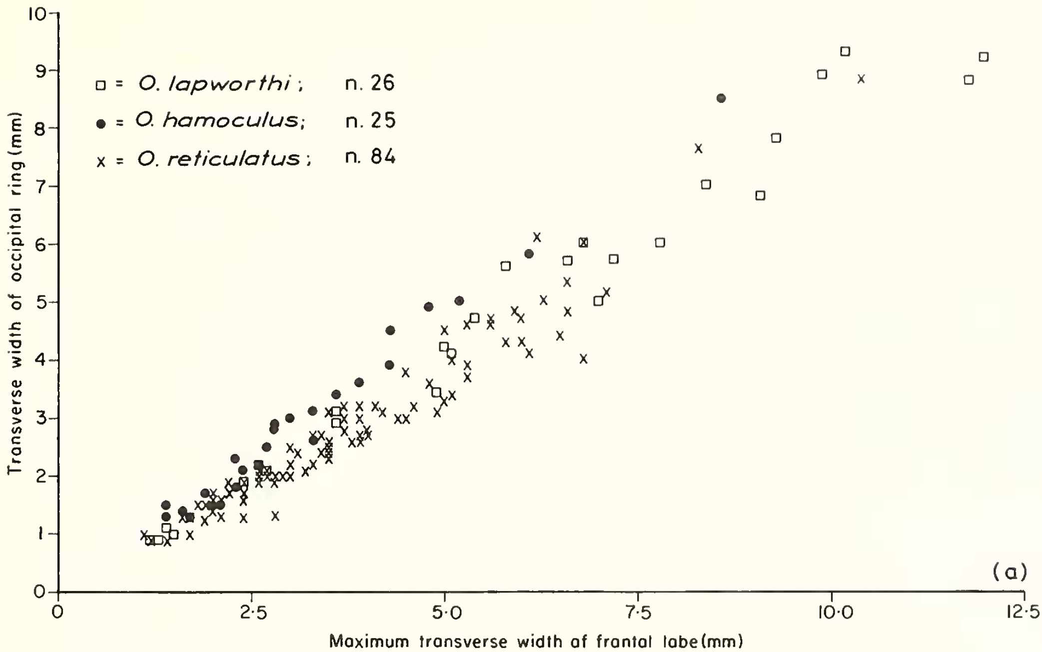
Elements of the faunal assemblage probably correlate with those from the younger part of the Lower Cambrian given in Fritz's (1972) *Bonnia–Olenellus* Zone, although the Scottish trilobite fauna is limited in its representation of genera. Fritz (1972, p. 7) lists genera that are commonly present in the zone as *Antagmus*, *Bonnia*, *Laudonia*, *Olenellus*, *Onchocephalus*, and *Zacanthopsis*. The base of the *Bonnia–Olenellus* Zone is placed by Fritz at the first appearance of *Olenellus*. The underlying *Nevadella* Zone contains the diagnostic genera *Bradyfallotaspis*, *Holmiella*, and *Nevadella* but *Olenellus* is, by definition, absent. *Olenellus* is also absent in strata overlying the *Bonnia–Olenellus* Zone.

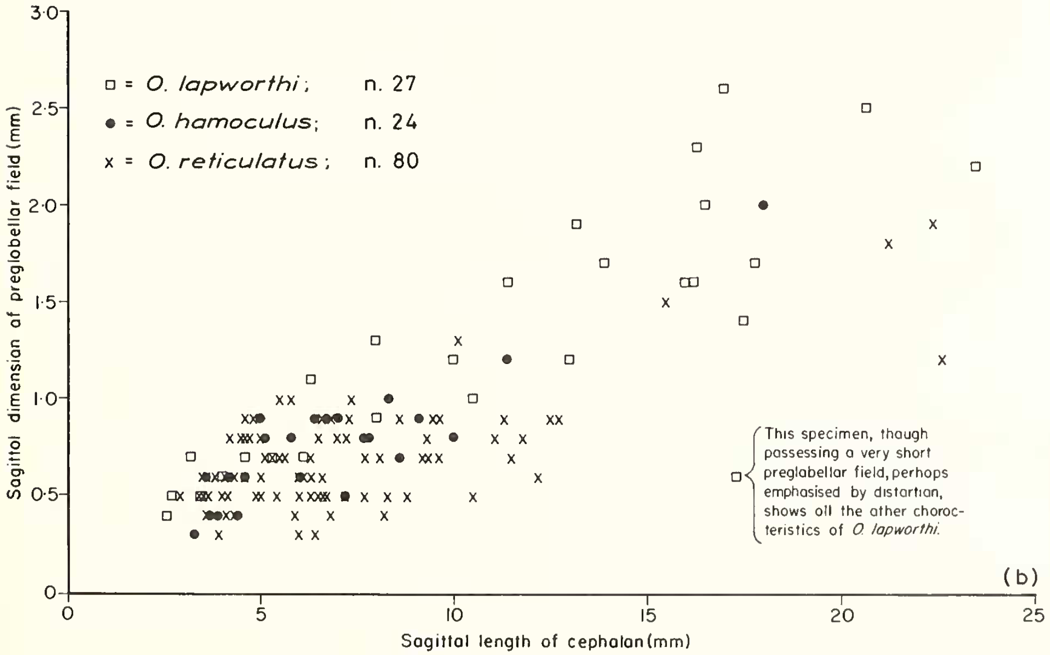


TEXT-FIG. 1. Part of north-west Scotland with selected fossiliferous Lower Cambrian 'Fucoid' Beds localities (National Grid references given) along the outcrop (shown diagrammatically by a black line) from Durness to Skye. 1, An-t-Sron, Loch Eriboll (NC 442 582); 2, Skiag Bridge (NC 235 245); 3, Loch Awe quarry (NC 251 158); 4, Knockan Cliff (NC 192 093); 5, Allt nan Righreon (NH 095 794) and Loch an Nid (NH 083 747); 6, Meall a'Ghiubhais, Kinlochewe (NH 979 655); 7, Ord, Skye (NG 613 122).



TEXT-FIG. 2*a*, *b*, differentiation of *O. lapworthi* from *O. reticulatus* and *O. hamoculus*.





TEXT-FIG. 3*a*, differentiation of *O. hamoculus* from *O. lapworthi* and *O. reticulatus*. *b*, relation of preglabellar field to sagittal cephalic length.

Age equivalence between the 'Fucoid' Beds of Scotland and the Bastion Formation of East Greenland (Cowie and Adams 1957) can be based on the faunas which include fairly closely comparable species of *Olenellus* from similar lithologies.

Specimens are lodged in the Institute of Geological Sciences, in Edinburgh (GSE) and in London (GSM), the British Museum Natural History (BM), and the Department of Geology, University of St. Andrews (F).

SYSTEMATIC PALAEONTOLOGY

Family OLENELLIDAE Vogdes, 1893
Genus OLENELLUS Billings, 1861

Type species. Olenus thompsoni Hall, 1859, from the Lower Cambrian of Georgia Township, Vermont.

Remarks. The relationship between *Olenellus* and *Paedeumias* has been discussed recently by Fritz (1972) and Cowie (1968). For the purposes of this paper the allocation of *Paedeumias* to *Olenellus* suggested by Fritz is accepted.

Olenellus lapworthi Peach and Horne, 1892

Plate 69, figs. 1-6

1892 *Olenellus lapworthi* Peach and Horne, pp. 227-242, pl. 5, figs. 2-4, 6.
?1892 *Olenellus lapworthi* Peach and Horne, pl. 5, figs. 7, 9, 10, 12, 13, *non* 11.
1894 *Olenellus lapworthi* Peach; Peach, pp. 662-664, pl. 29, fig. 1.
1894 *Olenellus lapworthi* var. *elongatus* Peach, p. 664, pl. 29, fig. 4.
1907 *Olenellus lapworthi* Peach and Horne; Peach *et al.* pp. 401, 404, 413, 415.
1910 *Olenellus lapworthi* Peach; Walcott, pp. 331-332, pl. 39, figs. 4-?6, *non* 1-3.
1937 *Olenellus lapworthi* Peach; Lake, pp. 238-240, pl. 33, fig. 10, *non* 11; pl. 34, figs. 1, 2, 5, *non* 3, 4, 6.

EXPLANATION OF PLATE 69

All specimens from the Fucoid Beds.

Figs. 1-6. *Olenellus lapworthi* Peach and Horne, 1892. 1, GSE 5364, internal mould of lectotype cephalon from Allt nan Righreon, Dundonnell; ×1·5. Figured by Peach and Horne 1892, pl. 5, fig. 2. 2, GSE 5360, latex cast of external mould of incomplete dorsal exoskeleton from Meall a'Ghiubhais, Kinlochewe; ×8. Figured by Walcott 1910, pl. 39, fig. 5. 3-5, GSE 13301, 13304, 13310, internal moulds of cephala from Loch Awe quarry, near Inchnadamph; ×3, ×2, ×2·5. 6, BM I 11189, internal mould of fragmentary dorsal exoskeleton showing impression of hypostome on glabella; from Meall a'Ghiubhais, Kinlochewe; ×2·5.

Figs. 7-15. *Olenellus reticulatus* Peach, 1894. 7, GSE 5343, internal mould of lectotype cephalon from same locality as Fig. 6; ×1·5. 8, BM I 11190, internal mould of hypostome from same locality as Fig. 6; ×3. 9, GSE 5344, internal mould of paralectotype cephalon from Allt nan Righreon, Dundonnell; ×1·5. Figured by Peach 1894, pl. 30, fig. 5. 10-12, GSE 13295, internal mould of cephalon from Loch Awe quarry, near Inchnadamph. Dorsal, left-lateral, and anterior views; ×2. 13, 14, GSE 13324, 13325, internal moulds of small cephala from same locality as figs. 10-12; ×4, ×3. 15, GSE 5342, external mould of paralectotype cephalon from Meall a'Ghiubhais, Kinlochewe; ×1. Figured by Peach 1894, pl. 30, fig. 2.

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1937 *Wanneria*? sp.; Lake, pp. 246–247, pl. 35, fig. 5.
1951 *Paedeumias hanseni* Poulsen; Poulsen, p. 161.
?1957 *Olenellus lapworthi* Peach; Palmer, p. 120.
1960 *Olenellus lapworthi* Peach; Kielan, p. 87.
1965 *Olenellus lapworthi* Peach; Brand, p. 286.
1972 *Olenellus lapworthi* Peach; Cowie *et al.*, p. 28.
1972 *Paedeumias hanseni* Poulsen; Cowie *et al.*, p. 28.
1974 *Olenellus lapworthi* Peach; Cowie, p. 136.
1974 *Paedeumias hanseni* Poulsen; Cowie, p. 136.

Lectotype. An incomplete cranidium, GSE 5364 (Pl. 69, fig. 1), from the 'Fucoid' Beds, Lower Cambrian at Allt nan Righreon (Allt Righ Ian) NH 095 794 near the hill-track 7 km south of Dundonnell, Ross and Cromarty, Scotland; figured by Peach and Horne (1892, pl. 5, fig. 2); herein selected.

Dimensions of lectotype.

	mm
Sagittal length of cephalon	17·5
Maximum width of cephalon	35·4
Sagittal dimension of preglabellar field	1·4
Sagittal length from anterior cephalic margin to anterior glabellar furrow (3p)	9·3
Exsagittal length of eye lobe	7·7
Exsagittal distance from posterior tip of eye lobe to posterior border of cephalon	2·5

Paralectotypes. Incomplete cephala GSE 458, GSE 457, GSE 456, GSE 5366, figured by Peach and Horne (1892, pl. 5, figs. 3–6 respectively); same horizon and locality as lectotype.

Material, horizons, and localities. Peach and Horne based this species on a small amount of poorly preserved, fragmentary material from Allt nan Righreon which was figured in their paper of 1892. In 1893 collections from Meall a'Ghiubhais gave better evidence. Though a little flattened in shale the fossils are quite well preserved and contain some complete specimens. *O. lapworthi* occurs a little more frequently at this locality than *O. reticulatus* Peach, 1894. Recent collections from the quarry at Loch Awe have yielded approximately twenty-five well-preserved cephala of *O. lapworthi* and numerous fragments; here this species is in a minority, comprising about 17% of the total number of well-preserved olenellid cephala. Thoracic segments are very rare and are almost invariably found isolated thus making their specific assignment difficult.

Diagnosis. Preglabellar field long; occupies one-fifth cephalic length in small specimens, one-tenth in long ones; frontal lobe well-rounded anteriorly; eye lobes are strongly curved and long, reaching at least as far back as the occipital ring; small inter-ocular area. Posterior border almost straight with genal angle in transverse line with occipital ring. Posterior of frontal lobe less than half cephalic length (*sag.*) from posterior of occipital ring. Exoskeleton faintly reticulated.

Description. Cephalon varies between semicircular (Pl. 69, fig. 3) and paraboloid (Pl. 69, fig. 4), the majority being semicircular; bordered by narrow, convex rim that slightly widens and flattens as it approaches genal angle. Posterior border very narrow at axial furrow, widening to genal angle; directed transversely out from axial furrow initially, then curving slightly forward distally to slightly advanced genal angle. Intergenal angle two-thirds posterior margin length from axial furrow; border thickens slightly at intergenal angle (Pl. 69, fig. 4). In immature specimens intergenal angle at half posterior width from axial furrow and genal angle in a more advanced position (Pl. 69, fig. 2). Genal spine continues line of lateral border, being directed slightly outward posteriorly; extends for over half length of cephalon. Glabella widest anteriorly narrowing to 1p furrow then slightly widening to occipital ring. Frontal lobe moderately convex and occupies more than half of glabellar length in large specimens, less than half in small ones; occupies one-quarter of cephalic width; well rounded frontally (Pl. 69, fig. 3); posterior situated at over half cephalic length from anterior border. Ratio of cephalon length to preglabellar and frontal lobe length varies between 1:0·53 and 1:0·59. The frontal lobe is almost equal to the width of the occipital ring. In *O. reticulatus* the frontal lobe is a little broader relatively. There are three pairs of glabellar furrows: 3p furrow transglabellar; directed strongly forward abaxially at 45°, then curves back through a right angle to direct backward as it enters axial furrow. 2p furrow not transglabellar; parallel to anterior furrow adaxially, but abaxially becomes divergent resulting in anterior glabellar lobe lengthening (*exsag.*) distally, nearly geniculate, then narrowing abruptly close to axial furrow; gently recurved backward at axial furrow where it abruptly shallows (Pl. 69, fig. 5). 3p and 2p furrows situated close to each other, resulting in 3p lobe being narrower (*sag.* and *exsag.*) than 2p lobe as 1p furrow is situated further from 2p furrow. 1p furrow not transglabellar; wider (*exsag.*) than anterior and median furrows, consisting of short, abaxially situated slits, directed gently forward (abaxially). Occipital furrow similar to posterior glabellar furrow. Node situated postero-medially on occipital ring (Pl. 69, fig. 1). Moderately long preglabellar field (Pl. 69, fig. 3) occupies one-tenth or more glabellar length in large specimens, up to one-fifth in small ones (Pl. 69, fig. 2). From postero-lateral part of frontal lobe eye lobe arches out strongly, making an angle of about 140° with frontal lobe. It is long (text-fig. 2*b*), occupying two-fifths cephalic length in mature specimens, one-half in small ones, strongly curved, wide (*tr.*) with a gently convex dorsal surface; well-curved inner edge, more strongly curved outer edge, eye lobe being furthest from glabella opposite 1p furrow; posteriorly terminates opposite and close to occipital ring, in some examples (Pl. 69, fig. 3) almost reaching posterior border; post-ocular cephalic length is about one-tenth total cephalic length (text-fig. 2*a*). Eye surface occupied outer edge of eye lobe, being now represented by a narrow furrow (Pl. 69, fig. 5). Shallow epipalpebral furrow is sometimes present. Inter-ocular area almost enclosed; small and slightly raised. Extra-ocular area broad, low, sloping very gently laterally. Hypostome is unknown. Thorax composed of fourteen segments (Pl. 69, fig. 6); third segment macro-pleural, being longer (*exsag.*) than any of other pleurae, and extended postero-laterally as long pleural spine. Axis tapers gradually posteriorly. In mature specimens (Pl. 69, fig. 6) pleurae (to fulcrum) occupies slightly more than one-third thoracic width anteriorly as they narrow (*tr.*) posteriorly more strongly than axis. In immature specimens pleurae occupy less than one-third thoracic width anteriorly. First, second, fourth, fifth pleurae develop very short spines laterally; those posterior to fifth segment develop longer pleural spines. Pleurae depressed medially, bounded anteriorly and posteriorly by raised pleural bands. Posterior axial ring bears long spine which is almost as long as thorax (Pl. 69, fig. 6).

Discussion. Peach's paper (1894), in which further species of *Olenellus* were described, illustrated specimens, many of them articulated, from the Fucoid Beds of Meall a'Ghiubhais, Kinlochewe. As suggested by Peach (1894) the specimens of *O. lapworthi* from Meall a'Ghiubhais are generally smaller than the *O. reticulatus* specimens but the converse is true at the Loch Awe locality. This species shows a small degree of intraspecific variation, as has been alluded to in the description; this involves small variation in length of preglabellar field (contrast Pl. 69, fig. 3 and Pl. 69, fig. 6), eye lobe (contrast Pl. 69, fig. 3 and Pl. 69, fig. 1), position of genal angle, and over-all cephalic shape (contrast Pl. 69, fig. 1 and Pl. 69, fig. 4). The specimens described by Peach and by Peach and Horne tend to be semicircular, but many collected from Loch Awe tend toward a more parabolic outline. Comparisons with other forms present in the Fucoid Beds will be made under the relevant discussions.

Other species similar to *O. lapworthi* are: *O. transitans* (Walcott, 1910), *O. thompsoni* (Hall, 1859), *O. hanseni* (Poulsen, 1932), and *O. svalbardensis* (Kielan, 1960). *O. transitans* can be distinguished by its narrower glabella and slighty longer eye lobe, more distally positioned intergenal angle, larger inter-ocular area and smaller frontal lobe (see Walcott 1910, p. 338), whilst *O. thompsoni*, another North American form, lacks a preglabellar field and possesses a broader border. *O. hanseni*, from the Lower Cambrian of Ella Island, East Greenland, is very similar to *O. lapworthi*, differing only in having a slightly longer eye lobe which reaches to the posterior border. *O. svalbardensis*, from the Slakli Series in Spitsbergen, possesses a shorter preglabellar field, broader and more advanced genal angle.

Olenellus reticulatus Peach, 1894

Plate 69, figs. 7–15; Plate 70, figs. 1, 2, 12

1892 *Olenellus lapworthi* Peach and Horne, pl. 5, figs. 1, 7, 8.
1894 *Olenellus reticulatus* Peach, pp. 665-666, pl. 30, figs. 1–5, ?6–14; pl. 31, figs. 1–7.
1894 *Olenellus lapworthi* Peach (pars.); Peach, pl. 29, figs. 2, 5.
1894 *Olenellus lapworthi* var. *elongatus* Peach (pars.), pl. 29, fig. 3.
1894 *Olenellus gigas* Peach, text-fig. 1, p. 667.
1907 *Olenellus reticulatus* Peach; Peach *et al.*, pl. 52, fig. 4, 4*a*, *b*.
1907 *Olenellus lapworthi* Peach; Peach *et al.*, pl. 52, figs. 2, 3.
1910 *Olenellus reticulatus* Peach; Walcott, pp. 335–336, pl. 39, figs. 8–13, ?14.
1910 *Olenellus lapworthi* Peach (pars.); Walcott, pl. 39, figs. 1–3.
1937 *Olenellus reticulatus* Peach; Lake, pp. 240–243, pl. 34, figs. 7–?9, 10, 11.
1937 *Olenellus lapworthi* Peach (pars.); Lake, pl. 34, figs. 1, 3, 4, 6.
?1937 *Wanneria* ?sp.; Lake, pp. 246–247 (pars.), pl. 35, fig. 4.
1951 *Wanneria nathorsti* Poulsen; Poulsen, p. 161.
1957 *Olenellus reticulatus* Peach; Palmer, p. 120.
1972 *Olenellus reticulatus* Peach; Cowie *et al.*, p. 28.
1972 *Wanneria nathorsti* Poulsen; Cowie *et al.*, p. 28.
1974 *Olenellus reticulatus* Peach; Cowie, p. 136.
1974 *Wanneria nathorsti* Poulsen; Cowie, p. 136.

Lectotype. An incomplete cephalon, GSE 5343 (Pl. 69, fig. 7), from the 'Fucoid' Beds, Lower Cambrian on the northern slopes of Meall a'Ghiubhais, 5·5 km WNW. of Kinlochewe, Ross and Cromarty, Scotland, figured by Peach (1894, pl. 30, fig. 1); herein selected.

Dimensions of lectotype.

	mm
Sagittal length of cephalon	25·5 (estimated)
Maximum width of cephalon	42·0 (estimated)
Sagittal dimension of preglabellar field	2·4
Sagittal length from anterior cephalic margin to anterior glabellar furrow (3p)	14·8
Exsagittal length of eye lobe	8·5
Exsagittal distance from posterior tip of eye lobe to posterior border of cephalon	—

Paralectotypes. Two incomplete cephala, GSE 5342 and GSE 5344, one incomplete articulated specimen, GSE 5350, and an incomplete thorax GSE 5351; same horizon and locality as lectotype; figured by Peach (1894, pl. 30, figs. 2, 4, 5; pl. 31, fig. 4 respectively).

Material, horizons, and localities. In addition to the numerous, well-preserved, though generally incomplete, cephala from the type locality at Meall a'Ghiubhais, this species has been found at Allt nan Righreon (Peach and Horne, 1892, pl. 5, fig. 1; this specimen has a shorter eye lobe than is evident from Peach and Horne's drawing). Recent collecting at the Loch Awe quarry (text-fig. 1) has yielded more than 100 well-preserved cephala and countless fragmentary specimens. This species occurs a little less frequently at Meall a'Ghiubhais than *O. lapworthi*, but at the Loch Awe quarry it comprises about 65% of the olenellid fauna. At all these localities it is restricted to the Fucoid Beds, Lower Cambrian.

Diagnosis. Preglabellar field short; frontal lobe tapered anteriorly. Eye lobes short, posterior tips being in line with 1p lobe and gently curved. Genal angle slightly advanced from normal position, distal part of posterior border is concave forward from intergenal to genal angle. Exoskeleton coarsely reticulate.

Remarks. This species differs from *O. lapworthi* in the following respects:

(*a*) preglabellar field shorter, occupying one-tenth cephalic length in small individuals, and more than one-tenth in large ones;
(*b*) frontal lobe tapers anteriorly (Pl. 69, figs. 14, 15); posterior set at one-half cephalic length from anterior margin;
(*c*) frontal lobe occupies one-third cephalic width in large individuals, and between one-third to one-quarter in small ones;
(*d*) eye lobe less strongly curved, making an angle of about 160° with the frontal lobe; short, extending for two-fifths cephalic length in small individuals, a little over one-third in large ones (text-fig. 2*b*); terminates opposite 1p lobe;
(*e*) postocular cephalic length is one-fifth cephalic length (text-fig. 2*a*);
(*f*) interocular area is broader posteriorly;
(*g*) genal angle slightly more advanced, distal part of posterior border being concave forward (Pl. 69, fig. 10);
(*h*) exoskeleton coarsely reticulated (Pl. 69, fig. 15);
(*i*) thoracic pleurae (to fulcrum) narrower anteriorly, being less than one-third axial width (Pl. 70, fig. 12).

Although having suffered some degree of distortion, the often paraboloid form of the cephalon is considered to be a real, not apparent effect. This is demonstrated by Plate 69, figs. 10–17, the specimen showing no flattening and little lateral compression, but having a paraboloid form. In Plate 69, fig. 15 the specimen is seen to have been flattened and consequently appears to be a little broader.

Hypostome (Pl. 69, fig. 8) is a little longer than broad. Anterior lobe strongly swollen, semicircular; occupies five-sixths hypostomal length. Medial furrow deep, curved gently convex posteriorly. Posterior lobe is very short and crescentic. Posterior border very narrow (*sag.*) medially, widens laterally into postero-lateral spine.

Discussion. Variation in cephalic shape has been noted and may be partly related to local environmental conditions; specimens from the Loch Awe quarry being characterized by a preponderance of more paraboloid forms, whilst those from Meall a'Ghiubhais tend to be more semicircular. Another variation which occurs between specimens from these two localities is in size; those from Loch Awe tending to be smaller than the associated *O. lapworthi* whilst at Meall a'Ghiubhais the converse is true (Peach 1894, p. 665). These two factors would seem to be interrelated, the cephalon being parabolic in small individuals, becoming more semicircular in the more mature stage (McNamara 1978, text-fig. 4). In large individuals of *O. reticulatus* the genal angle is positioned a little further forward than in less mature individuals. The difference between the posterior border in large forms of this species and large forms of *O. hamoculus* lies in the distal section; in *O. reticulatus* it is concave forward whilst in *O. hamoculus* it is convex forward. The shallow epipalpebral furrow (Pl. 69, fig. 10 and Pl. 70, fig. 1) extends into the frontal lobe as a single furrow and does not appear to bifurcate as in the olenellid *Wanneria ?lundgreni* (Moberg) figured by Bergström (1973, figs. 1, 17, 18*d*).

The possibility that *lapworthi* and *reticulatus* are sexual dimorphs has been examined but because of the above and other factors (see McNamara 1978) there seem to be no firm grounds for invoking this speculation.

One specimen of *O. reticulatus* has an indented genal angle (Pl. 70, fig. 2). This was not caused by post-ecdysial mechanical breakage because the raised cephalic border is intact and follows the line of the indentation. Thus the border had been regenerated after the living trilobite had lost its genal spine and postero-lateral genal area, probably from having been attacked by a predator, perhaps shortly after ecdysis. Burling (1916) described and figured a specimen of *O. robsenensis* with healed, broken pleurae in a position a little posterior to that of the *O. reticulatus* specimen. The shortness of the eye of *O. reticulatus* may account for the damage to the genal angle. From the position of the furrow on the distal part of the eye lobe which carried the eye surface, it can be inferred that, as the eye surface did not extend to the very posterior tip of the eye lobe, the horizontal range of vision was approximately 80°, ranging from just in front of the genal angle to a point on the border in line (*tr.*) with the middle of the frontal lobe. Thus this species could have been vulnerable to attack from the posterior, so perhaps accounting for the injured parts being in a similar position in both the Scottish specimen and Burling's specimen.

What Peach (1894, p. 665, fig. 2) considered to be the telson of this species is in fact an extended axial spine borne, in *O. reticulatus*, by the fourteenth thoracic segment. An opisthothorax and true telson have not been observed in this species.

O. reticulatus bears very short eye lobes in comparison to many species of *Olenellus*, though *O. truemani* Walcott, 1913, *O. fremonti* (Walcott, 1910), and some individuals of *O. gilberti* Meek, 1874 also have short eye lobes. Although the eye lobes of *O. truemani* are of similar length to those of *O. reticulatus*, they are broader; it also has a shorter preglabellar field. *O. fremonti* has both short eye lobes and an advanced genal angle, but its frontal lobe abuts against the anterior border. The form from the Eager Formation in Canada referred by Best (1952) to *O. gilberti*, has eye lobes as short as those of *O. reticulatus*, a distinct preglabellar field and slightly advanced genal angle. The difference between the two species lies in the extraocular area which is much narrower in *O. reticulatus* as the glabella is proportionately broader. Poulsen (1951) referred a specimen of *O. reticulatus* to *Wanneria nathorsti* Poulsen (1932), from the Ella Island Formation, East Greenland, but *W. nathorsti* possesses a much broader border and lacks a preglabellar field.

O. gigas is considered to be a large specimen of *O. reticulatus*. The specimen

(GSE 467) figured by Peach (1894, text-fig. 1, p. 667), Walcott (1910, pl. 40, fig. 1), and Lake (1937, pl. 35, fig. 3) has prominent reticulation, short, gently curved eye lobes, the posterior tip of which was probably in line with the 1p as in *O. reticulatus*. The anterior of the specimen is very poorly preserved thus the dimensions of the preglabellar field cannot be ascertained.

Olenellus hamoculus sp. nov.

Plate 70, figs. 3–9

Derivation of name. Hamus—hooked; oculus—eye.

Holotype. Complete cephalon, GSE 13302 (Pl. 70, fig. 3), from the 'Fucoid' Beds, Lower Cambrian, Loch Awe, Sutherland. The locality is a roadside quarry 170 m E. 10° S. of the north-eastern inlet of Loch Awe (NC 251 158).

Dimensions of holotype.

	mm
Sagittal length of cephalon	10·0
Maximum width of cephalon	18·0
Sagittal dimension of preglabellar field	0·8
Sagittal length from anterior cephalic margin to anterior glabellar furrow (3p)	5·3
Exsagittal distance from posterior tip of eye lobe to posterior border of cephalon	2·9

Paratypes. Six cephala GSM 102276, GSE 13305, GSE 13300, GSE 13298, GSE 13303, GSE 13307, same horizon and locality as holotype.

Material, horizon, and locality. Twenty-five well-preserved and numerous fragmentary cephala are known from the type locality in the 'Fucoid' Beds at Loch Awe.

Diagnosis. Cephalon generally sub-ellipsoidal; anterior border almost transverse to gently rounded; genal angle advanced; distal part of posterior border convex forward. Frontal lobe is well rounded and approximately same width as occipital ring (text-fig. 3*a*); posterior of frontal lobe less than half cephalic length from anterior border. Eye lobes short, strongly curved, and broad.

Description. Cephalic outline varies between sub-semicircular, particularly in young forms (Pl. 70, figs. 4, 6) and sub-ellipsoidal in more mature forms (Pl. 70, fig. 3); anterior border nearly straight adaxially; bordered by narrow, rounded rim which flattens and widens only slightly towards genal angle. Posterior border less convex than anterior border; directed almost straight out from axial furrow then, half-way to genal angle in mature specimens (Pl. 70, fig. 3), slightly less than half-way in small cephala (Pl. 70, fig. 6), directed sharply forward in a forwardly convex curve, forming an intergenal angle of approximately 150°, the genal angle thus being in an advanced position level with or generally forward of the occipital furrow. At intergenal angle there is a thickening of the border which, in some specimens, develops into a small posteriorly directed node (Pl. 70, fig. 9). Genal spine half as long as cephalon; continues line of postero-lateral border. Glabella 'hour-glass' shaped, frontal lobe being of similar width (*tr.*) to occipital ring (text-fig. 3*a*); slightly vaulted transversely; occupies one-quarter width of cephalon. Posterior of frontal lobe situated at more than half cephalic length (*sag.*) from posterior of occipital ring. Anterior frontal lobe declines into a short preglabellar field which occupies slightly under one-tenth total cephalic length in large individuals, and slightly more than one-tenth in small ones (Pl. 70, fig. 4). Glabella bears three pairs of glabellar furrows: 3p furrow transglabellar; directed gently forward abaxially, then strongly recurved back around lateral extremity of 3p lobe; 2p furrow set close to 3p furrow, though it is less strongly recurved distally; 1p furrow, which is only faintly transglabellar, is set further back from 2p furrow than that is from 3p furrow. Flat central glabellar area, one-quarter posterior-glabellar width, is present between gently convex 1p lobes (Pl. 70, figs. 5, 8). Occipital furrow is similar to 1p furrow, though it is not transglabellar. Occipital ring as long (*sag.* and *exsag.*) as 1p lobe; bears a prominent node postero-medially (Pl. 70, figs. 3, 9). Posterior half of ring lies behind line of posterior border. From postero-lateral part of frontal lobe, eye lobe arches out strongly, making an angle of about 140° with frontal lobe; it is short, occupying one-third of cephalic length (text-fig. 2*b*), and broad; it has a strongly curved outer margin but a less strongly curved inner one; posterior tip recurves towards glabella, being situated opposite mid-point of 1p lobe (Pl. 70, fig. 9). Post-ocular cephalic length is one-fifth total cephalic length (text-fig. 2*a*). In one specimen (Pl. 70, fig. 9) there is a faint intergenal ridge extending to intergenal angle. Epipalpebral furrow well developed, particularly in mature specimens; continues faintly into frontal lobe (Pl. 70, figs. 6, 9). Interocular area small, slightly raised above extraocular level, which is wide, almost flat, gently downsloping to narrow border furrow. Other parts are unknown.

Discussion. O. hamoculus is distinguished from *O. lapworthi* in the following ways:

(*a*) the cephalon tends toward a sub-ellipsoidal shape, whereas it is sub-parabolic to sub-semicircular in *O. lapworthi*;

(*b*) the posterior border has a sharp intergenal angle with concomitant well advanced genal angle, whereas it is straight out to much more distally placed intergenal angle in *O. lapworthi*. The genal angle is hardly advanced in *O. lapworthi*;

(*c*) eye lobe shorter and more strongly curved.

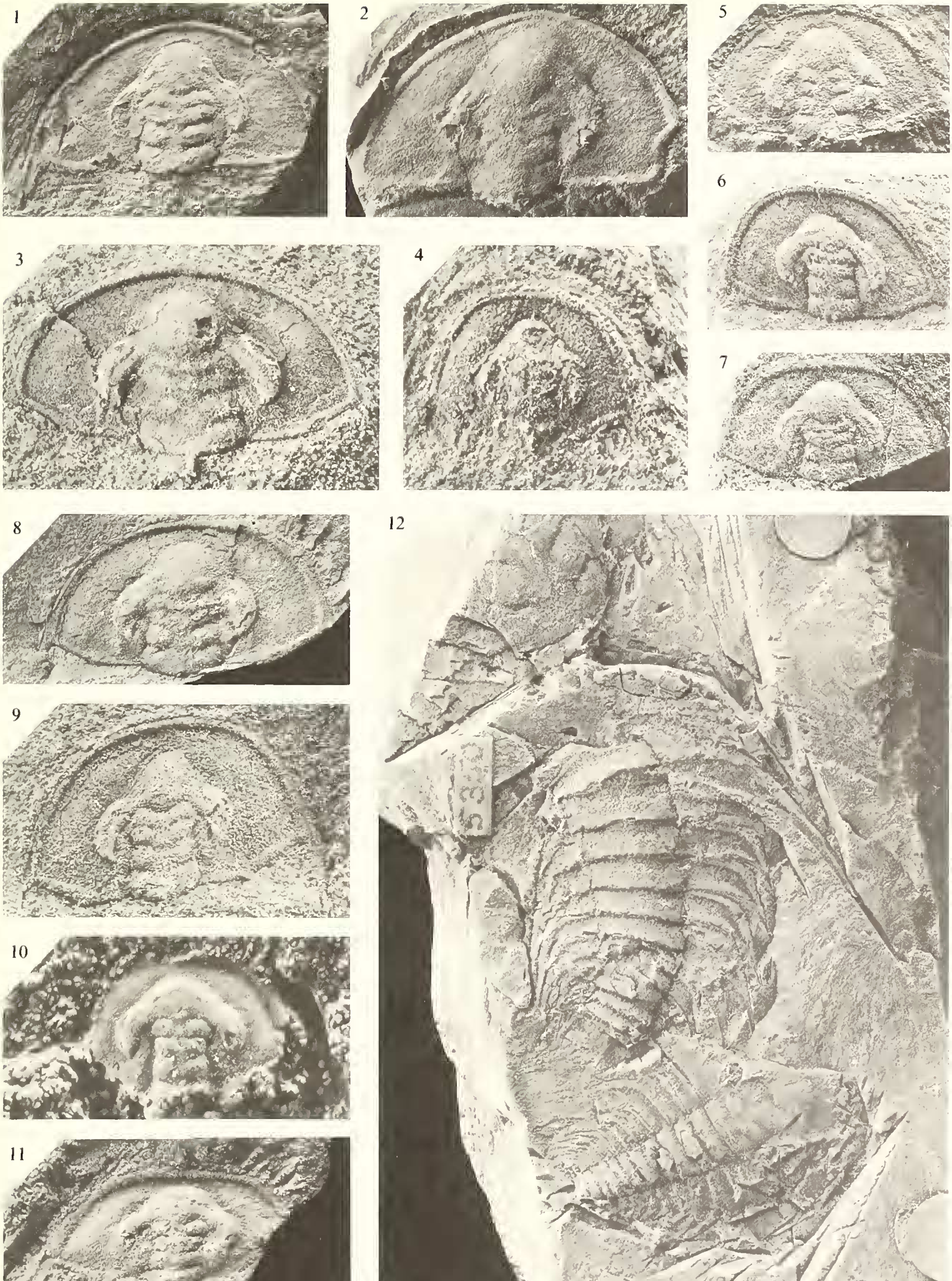
EXPLANATION OF PLATE 70

All specimens from the Fucoid Beds except F17 (fig. 10).

Figs. 1, 2, 12. *Olenellus reticulatus* Peach, 1894. 1, GSE 5372, internal mould of cephalon from Meall a'Ghiubhais, Kinlochewe; ×2. Figured by Lake 1937, pl. 34, fig. 1. 2, GSE 13309, internal mould of cephalon from Loch Awe quarry, near Inchnadamph; showing a healed wound of the cephalic border; ×2·5. 12, GSE 5350, two incomplete dorsal exoskeletons from same locality as fig. 1; ×2. Figured by Peach 1894, pl. 30, fig. 5.

Figs. 3–9. *Olenellus hamoculus* sp. nov., internal moulds of cephala from Loch Awe quarry, near Inchnadamph. 3, GSE 13302, holotype; ×3. 4, GSE 13305, paratype; ×5. 5, GSE 13303, paratype; ×4. 6, GSE 13300, paratype; ×4. 7, GSE 13307, paratype; ×3. 8, GSE 13298, paratype; ×2·25. 9, GSM 102276, paratype; ×4·25.

Figs. 10, 11. *Olenellus intermedius* Peach 1894. 10, F17, silicified incomplete cephalon from the *Salterella* Grit, Skiag Bridge; ×7. 11, GSE 5367, internal mould of cephalon from Meall a'Ghiubhais, Kinlochewe; holotype; ×6. Figured also by Lake 1937, pl. 35, fig. 1.



COWIE and McNAMARA, *Olenellus*

O. hamoculus is distinguished from *O. reticulatus* in the following ways:

(*a*) the eye lobe is more strongly curved (contrast Pl. 70, figs. 2, 3);
(*b*) the frontal lobe is more rounded anteriorly and its posterior is situated more anteriorly;
(*c*) the genal angle is in a more advanced position, the distal part of the posterior border being convex forward, not concave forward as in *O. reticulatus.*

A species of *Olenellus* which is morphologically similar to *O. hamoculus* is *O. eagerensis* Best, 1952, from the Eager Formation, British Columbia. It compares in having the well-advanced genal angle, short, hooked eye lobe, 'hour-glass' shaped glabella, and almost transverse anterior border. The differences lie in the preglabellar field, which is not present in *O. eagerensis*, and the frontal lobe, which is not as strongly swollen in *O. hamoculus.* The similarities between these two species is probably a reflection of their occupation of similar niches (McNamara 1978) and does not indicate any inherent close genetic relationship as they were geographically widely separated (Cowie 1971, figs. 1, 4).

Similarity can also be noted between *O. hamoculus* and *O. mohavensis* (Crickmay, 1933) from Lower Cambrian shales in the Mohave Desert, California, U.S.A., which has slightly longer and less strongly curved eye lobe; shorter preglabellar field and frontal lobe almost touching anterior rim, even in immature individuals.

Olenellus intermedius Peach, 1894

Plate 70, figs. 10, 11

1894 *Olenellus intermedius* Peach; pp. 666–668, pl. 32, fig. 7.
1910 *Olenellus intermedius* Peach; Walcott, p. 332.
1937 *Olenellus*? *intermedius* Peach; Lake, pp. 244–245; pl. 35, fig. 1, *non* 2.

Holotype. Holotype is by monotypy. An almost complete cephalon, GSE 5367, from the 'Fucoid' Beds, Lower Cambrian, Meall a'Ghiubhais, Scotland, figured by Peach 1894, pl. 32, fig. 7.

Dimensions of holotype.

	mm
Sagittal length of cephalon	3·0
Maximum width of cephalon	7·0
Sagittal dimensions of preglabellar field	0·15
Sagittal length from anterior cephalic region to anterior glabellar furrow (3p)	1·3
Exsagittal length of eye lobe	0·9
Exsagittal distance from posterior tip of eye lobe to posterior border of cephalon	1·0

Material, horizons, and localities. In addition to the holotype one other cephalon is known from the same horizon and locality as the holotype. The cephalon which Lake (1937) referred to this species is a small meraspid cephalon (1·2 mm, sagittal length) of *O. reticulatus.* A third, silicified, specimen (Pl. 70, fig. 10) is known from the *Salterella* Grit at Skiag Bridge (text-fig. 1).

Diagnosis. Anterior margin almost transverse; eye lobes short; preglabellar field very short; frontal lobe short (*sag.*); extraocular area narrow; intergenal angle close to axial furrow. Glabellar furrows nearly transverse; none are clearly transglabellar, but sometimes a very faint connection across the glabella can be seen.

Description. Cephalon hexagonal shaped, broader than long; border almost transverse anteriorly; genal angle advanced, being in line with 1p lobe. Intergenal angle set approximately one-third distance from axial furrow to genal angle; bears a short spine which continues as the raised intergenal ridge which traverses cheek in a gentle curve and meets axial furrow by 1p lobe; posterior furrow which demarcates this intergenal ridge more pronounced than anterior one. Preglabellar field very short, being one-twentieth the cephalic length in the holotype (Pl. 70, fig. 11).

Glabella widest anteriorly across frontal lobe, narrowing at 2p furrows, then widening slightly to occipital ring. Frontal lobe short, occupying two-fifths glabellar length. 3p furrow curved; 2p furrow nearly straight and transverse; 1p furrow slightly curved, running a little backward adaxially; none of the furrows is transglabellar. Occipital furrow transverse and shallow medially, runs slightly forward abaxially and is deeper. Occipital ring bears prominent occipital node. Eye lobe arches strongly from the frontal lobe but is gently curved and short, occupying a little under one-third cephalic length; posterior tip in line with 1p furrow. Interocular area is slightly swollen. Extraocular area narrow; flat close to eye lobe, gently declines both laterally and posteriorly. Marginal furrow is moderately impressed.

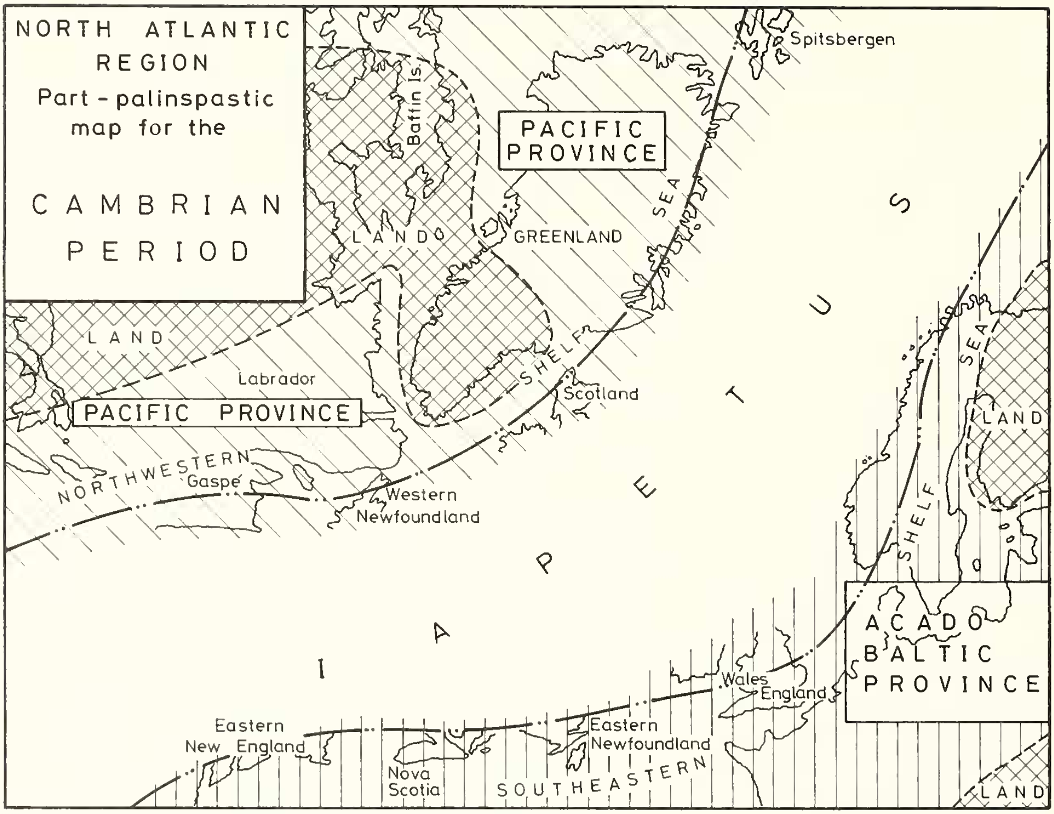
Discussion. Walcott (1910, p. 332) considered *O. intermedius* to be an immature form of *O. lapworthi* on account of the advanced position of the genal angle. The young forms of *O. lapworthi* 2–3 mm in length, though tending to have a more advanced genal angle than the mature form, possess a long eye lobe which, as in more mature forms, reaches to the occipital ring; so *O. intermedius* cannot be considered a young form of *O. lapworthi.* Lake (1937, pp. 244–245) placed the species questioningly within the genus *Olenellus* and included within it a specimen which had earlier been figured by Walcott (1910, pl. 39, fig. 8) and considered by him to be a young form of *O. reticulatus.* The specimen, though broken and very poorly preserved, has a longer eye lobe than *O. intermedius*, the posterior tips being in line with the 1p lobe; thus, as Walcott suggested, it probably represents an immature form of *O. reticulatus.*

Both Walcott and Lake either questioned the validity of this species or were uncertain as to its true generic position, but the discovery of two further specimens would appear to validate the species. It is most closely related to *O. hamoculus* which has a similarly advanced genal angle but differs in possessing shorter, less strongly curved eye lobes, more transverse anterior cephalic border, and shorter (*sag.*) preglabellar field.

Bristolia bristolensis (Resser, 1928) and *B. insolens* (Resser, 1928) from the Lower Cambrian of Nevada similarly have a short eye lobe, glabella impinging against the anterior border, and almost transverse 2p furrow, but the anterior two pairs of glabellar furrows are transglabellar, the eye lobe lies much closer to the glabella, and the genal angle is in a far more advanced position.

SIGNIFICANCE, PALAEOGEOGRAPHIC AND BIOGEOGRAPHIC RELEVANCE OF THE FAUNA

The olenellid fauna of the Fucoid Beds is undoubtedly a North American Pacific Province association and the zonal significance is probably to date the 'Fucoid Beds' as in the younger part of the Lower Cambrian—the *Bonnia–Olenellus* Zone (Fritz 1972). Deposition of the Fucoid Beds will have thus been in the north-western shelf sea (text-fig. 4).



TEXT-FIG. 4. Part-palinspastic map for the Cambrian Period of the north Atlantic region. The barrier between the Pacific and Acado-Baltic Provinces of the Olenellid Realm, possibly deeper water of the Iapetus Ocean, is of unknown width and is not intended to be to any scale.

The faunal provinces of the Lower Cambrian of arctic North America, Greenland, Spitsbergen, and Scotland have been discussed by Cowie (1960, 1971) and Palmer (1969, 1972, 1973, 1974). The Olenellid Realm is divided into: (1) the Acado-Baltic Province with characteristic trilobites which include *Callavia*, *Holmia*, *Kjerulfia*, *Strenuaeva*, and *Strenuella*, and (2) the Pacific Province with characteristic trilobites which include *Bathynotus*, *Bonnia*, *Bonniella*, *Nevadia*, *Nevadella*, *Olenellus*, and *Protypus*.

In text-fig. 4 a palaeogeographical reconstruction has been made for the Cambrian Period which may be close to the Lower Cambrian situation. On this interpretation the Acado-Baltic Province was separated from the Pacific Province by the ancient ocean of Iapetus (Harland 1973; Harland and Gayer 1972). The faunal provinces would then lie on either side of this geographical barrier which prevented mixing of elements of the two provinces. North-west Scotland would have been on the north-west side of Iapetus with Greenland, Spitsbergen, and maritime Canada.

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